THE TALITROIDEAN AMPHIPOD GENUS *HYALE* RATHKE, 1837, SENS. STR. IN THE NORTH ATLANTIC AND MEDITERRANEAN REGIONS

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ABSTRACT

The genus *Hyale* Rathke, 1837, is here restricted to aquatic, non-saltatory hyalid amphipod species of the North Atlantic and Mediterranean regions. *Hyale pontica* Rathke, 1837 (type species) and *H. lubbockiana* Bate, 1857 are redescribed and *H. michelini* n. sp. (Sardinia) and *Hyale* species (Bermuda) are newly described. This complex of species is distinguished by unique features of gnathopod 1 (male) and preamplexing notch of peraeon segment 2 (female), posterior marginal cusps of coxae 2 & 3, and a strong striated clasping spine distally on the propod of peraeopods 3-7.

Introduction

During the course of study of hyalid amphipods of the North American Pacific coast, Bousfield & Hendrycks (2002) encountered a number of characters and character states on the basis of which generic subdivision of *Hyale* Rathke (sens. lat.) seemed advisable. Some of these had not hitherto been treated in the generic type species *Hyale pontica* Rathke, 1837. As material of the type species was not available to them, E. L. Bousfield contacted the first author of the present paper who had recently published comprehensively on the Mediterranean hyalid fauna and was able to re-examine extensive collections of *H. pontica* and similar species in the museum at Verona, Italy, and elswhere. These species were soon discovered to form a closely related clade, very distinct from other assemblages (e.g., "*grandicornis*" group) within the generic complex *Hyale* Rathke (sens. lat.). Since members of this complex are apparently confined to the North Atlantic and Mediterranean regions, and entirely extralimital to the North Pacific, a separate publication for this group was deemed advisable.

The type species *Hyale pontica* Rathke, 1837, was described originally from the coast of the Krym (Crimean) peninsula, Black Sea. Since that time, workers who found a *Hyale*-like animal with characteristically strong, robust, striated spine on the distal end of peraeopodal propods, were convinced they were dealing with this same species, be it from the Mediterranean or the eastern North Atlantic Ocean. As in many other similar cases, a striking and easily visible character often leads to a quick identification, without careful further examination and, in a second step, to being labelled as a "cosmopolitan" species. A second species of this group had been been described from the British Isles as *Galanthis lubbockiana* by Bate, 1856. Because of the "cosmopolitan syndrome", this species had been synonymized with *Hyale pontica* Rathke by many subsequent workers (e.g., Stebbing 1906; Chevreux & Fage 1925; Gurjanova 1951; Bulycheva 1957; Lincoln 1979; Barnard & Karaman 1991; and Krapp-Schickel 1993). G.O. Sars (1890) was a notable exception, maintaining separate identity of *H. lubbockiana* based on material from Norway. Further taxonomic disparities were more recently noted in material at hand from the Mediterranean region and Bermuda.

The purpose of this study is to unravel the true identity of the various species within the *Hyale pontica* complex, and describe new forms, based on character states both newly discovered and previously utilized. Hyalid amphipod collections in the Verona Museum contain a beautiful mating pair of animals from the Bosphorus (entrance to the Black Sea). Thus, character states of the true *Hyale pontica* Rathke could be established and differences with other material worked out.

Acknowledgments

The authors are grateful to: Wim Vader and colleagues at the Trømso Museum who checked fresh material of *Hyale lubbockiana* from Norwegian shore localities; Eric Laso-Wasem, Yale Peabody Museum, and Kathryn Coates, Bermuda Biological Station, for assisting in identification of B. M. Kunkel's original material of "*Hyale pontica*" (1910); and Aldo Michelin for many years of collaboration at the Museo Civico di Storia Naturale Verona. Sandro Ruffo generously provided laboratory facilites for part of the work, and gave his knowledgeable encouragement to the study. We sincerely thank Ed Hendrycks and Judith Price, Canadian Museum of Nature, and research assistant Pierre Marcoux, for their help in preparing, cataloguing, and illustrating some of the material. Floy E.

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Zitten, Cupertino, California, assisted with illustration of material from Bermuda. Marjorie Bousfield, Wolfe Island, ON, provided translations of the Russian literature.

Methods

Abbreviations of Agency collections used:
CMN - Canadian Museum of Nature, Ottawa
MSNV - Verona Museum, Italy
ROM - Royal Ontario Museum, Toronto
YPM - Yale Peabody Museum, New Haven , CO,

Abbreviations used in the text:

A1, 2	-	antennae 1, 2
BR SET	-	brood seta
CL	-	clasping
EP 1-3	-	epimeral plates 1, 2, 3
FLAG	-	flagellum
GDN	-	guiding
GN 1,2	-	gnathopods 1, 2
HD	-	head
IP	-	inner plate
LFT	-	left
LL	-	lower lip
MD	-	mandible
MX1,2	-	maxillae
MXPD	-	maxilliped
OP	-	outer plate
P-AMP NTCH	-	preamplexing notch on peraeon 2
P3-7	-	peraeopods
PLP	-	palp
RT	-	right
SP	-	spine
U1-3	-	uropods 1, 2, 3
UL	-	upper lip
UROS	-	urosome
T	-	telson

Systematics:

Rathke (1837) established the genus *Hyale* after having described his type species *H. pontica* from the Black Sea. Shortly afterwards, Bate (1857) described, under several different generic names, a similar species, *lubbockiana*, from the British Isles. It seems that Stebbing must have seen material of *lubbockiana* and thought it identical with *Hyale pontica* Rathke as well as *H. lubbockiana* Bate. He synonymized them, keeping the older name of course. In 1893 Della Valle offered drawings of "*lubbockiana*" and "*pontica*", but he mixed material of *nilssoni* as well as *Micropythia carinata*, and the drawings are not pertinent to the Atlantic species *H. lubbockiana*.

In 1906 Stebbing redescribed the female of "*pontica*". Chevreux& Fage (1925) cite "*pontica*" from the Atlantic and from the Mediterranean coast of France. In a paper on Mediterranean (Marseilles) species of *Hyale*, Giovannini (1965) provided detailed drawings (the text has some errors) of ?*pontica* that may be the most clearly executed until now. Mateus & Mateus (1966) stressed the necessity of a revision of all genera of families Hyalidae and Hyalellidae before the abundant material of the Calypso expedition could be worked up. Thus, in Lincoln's (1979) figures of "*pontica*" from the British Islands, palmar corners are very weak in gnathopods 1, 2 (♀) and peraeopods, while there is a clear corner in those of Chevreux & Fage's table (♂ 6mm). Finally, Krapp-Schickel (1993) fully treated material of *pontica* from the Mediterranean Sea.

Family Hyalidae Bulycheva 1957, revised Bousfield & Hendrycks 2002
Subfamily Hyalinae Bousfield & Hendrycks, 2002

Hyale Rathke sens. str.

Hyale Rathke, 1837: 377.
Hyale (part):Stebbing 1906: 559;—Chevreux & Fage 1925: 280;—Gurjanova 1951: 816;—Bulycheva 1957: 83;—Lincoln 1979: 230;—Krapp-Schickel 1993: 728;—Barnard & Karaman 1991: 367.
non *Nicea* Nicolet 1849 (type species *N. lucasi* Nic.)

Type species: *Hyale pontica* Rathke, 1837, present designation.

Species: *Hyale pontica* Rathke, 1837 (p. 3); *H. lubbockiana* Bate, 1856 (p. 6); ***H. michelini*** n. sp. (p. 9); *Hyale* species (Bermuda) (p. 11).

Diagnosis: Body smooth, or segments weakly imbricated or weakly mid-dorsally carinate. Rostrum inconspicuous; anterior head lobe subtruncate. Eye subovate. Antennae short, slender, subequal. Antenna 1, peduncular segment 2 > segment 3. Antenna 2, peduncle not incrassate; flagellum not elongate.

Upper and lower lips regular. Mandible, left lacinia 5-51/2 dentate, spine row with 3-5 blades. Maxilla 1, palp 1-segmented; outer plate, apical spine-teeth tall. Maxilliped, inner plate tall; palp normal, segment 3 short, medium thick; dactyl small, not falcate, unguis regular to elongate.

Coxae 2 and 3 with prominent sharp posterior marginal cusp, lacking in coxae 1 and 4. Coxa 5 markedly anterolobate; 6 & 7 posterolobate. Coxal gills medium, rounded, sac-like, largest on peraeopod 5.

Gnathopods sexually dimorphic. Gnathopod 1 (♂), propodal palm short, variously overhung by simple dactyl; carpal lobe narrow; propod with mediofacial guiding (bracing) spine; dactyl simple. Gnathopod 2 (♂), basis with strong anterodistal lobe (= hydrodynamic lobe of Bousfield & Hendrycks 2002); carpal lobe lacking; propod large, narrowing distally, palm with slight hinge tooth.

Peraeopods short, stout; bases expanded, posterior margins crenulate, hind margins of peraeopods 5 and 6 with weak surge seta and notch. Peraeopod 5, segment 4 short, broad; segment 5 often short; segment 6 with single large striated subterminal anterodistal clasping (locking) spine, and 1-2 small accessory spines; dactyl large, smooth, anterior marginal seta small.

Epimeral plates 1-3 regular, 3 not produced. Pleopods regular, natatory. Uropods 1 and 2, peduncle and rami short, thick. Uropod 1, distal peduncular spines short, unspecialized; rami with medium apical and marginal spines. Uropod 3 short, thick, uniramous; ramus shorter than peduncle, with apical spines only.

Telson broad, lobes slightly longer than broad, margins weakly setose.

Female: Gnathopods normal, subsimilar; carpal lobes shallow. Gnathopod 2 the larger; basis with stronger hydrodynamic lobe. Brood plates broadly subovate, apices rounded; marginal setae medium-long, hook-tipped. Peraeon 2, preamplexing notch large, rectangular, lacking unguisial groove, with small locking slit above anterior margin of notch.

Distributional Ecology: Open surf coasts of the Mediterranean and Black Seas; northeastern Atlantic, including Great Britain, and Norway, also Bermuda; clinging to algae and other substrata at LW level and subtidally to 50 m.

Remarks: Species of *Hyale* sens. str. differ markedly from those of *Apohyale* (Bousfield & Hendrycks, 2002) in being mainly aquatic and subtidal. They occur mostly in strongly lotic waters of open surf coasts, and saltate (hop) in air weakly or not at all (see Sars 1890). Mature females of *Hyale* possess regularly rounded brood plates with longish marginal hooked setae, whereas those of *Apohyale* have very broad, apically acute brood plates with numerous short marginal hook-tipped setae.

Species of *Hyale* are apparently uniquely adapted to a life style in strongly lotic waters such as the surf zone of open coasts. Thus, the tip of the large propodal median facial guiding spine (♂) appears to fit into a locking slit on peraeon 2 (♀), thereby enhancing the grip of the gnathopod when the dactyl closes on the preamplexing notch. In apparent homoplasious manner, the preamplexing mechanism within genus *Hyale* resembles that of some species within genus *Allorchestes* (e.g., *A. angusta* Stebbing)(family Hyalellidae).

Hyale pontica Rathke, 1837
(Figs. 1,2,3)

Hyale pontica Rathke, 1837: 378, pl. 5, fig. 20-28;—Bulycheva 1957: 90-92, fig. 30;—Krapp-Schickel 1993: 735-736, fig. 503.

Hyale pontica (part): Stebbing 1906: 568;—Barnard & Karaman 1991: 369.

non *Hyale pontica* Kunkel 1910: 69, fig. 26;—Chevreux & Fage 1925, fig. 294;—Lincoln, 1979: 236, figs. 109 e-j.

Key to species of *Hyale* Rathke, 1837 sens. str.

1. Antenna 2 (♂), flagellar segments with groups of dense setae; peraeopods 5-7, large clasping spine inserted diagonally proximad; peraeopod 5, segment 5 not wider than long ..... *H. pontica* Rathke (p. 4)
   Antenna 2 (♂), flagellar segments with single setae; peraeopods 5-7, large clasping spine inserted nearly perpendicular to axis of segment 6; peraeopod 5, segment 5 short, wider than long ..... 2.

2. Peraeopods 5-7, clasping and distal supernumary spine separated by cluster of 3-5 setae ..... ***Hyale*** sp. (p. 11)
   Peraeopods 5-7, clasping and distal supernumary spine separated by 1-2 setae ..... 3.

3. Gnathopod 1 (♂), carpal lobe small, not surpassing merus, distal margin with 3-4 short comb setae; maxilla 1, inner plate, apical plumose setae surpassing base of apical spines of outer plate; maxilliped palp segment 4 (dactyl), unguis with elongate nail ..... ***H. michelini*** n. sp. (p. 9)
   Gnathopod 1(♂), carpal lobe large, extending beyond merus, distal margin with 6-7 comb setae; maxilla 1, inner plate, apical plumose setae not exceeding base of apical spines of outer plate; maxilliped palp, unguis normal, shorter than body of dactyl ..... *H. lubbockiana* (Bate) (p. 6)

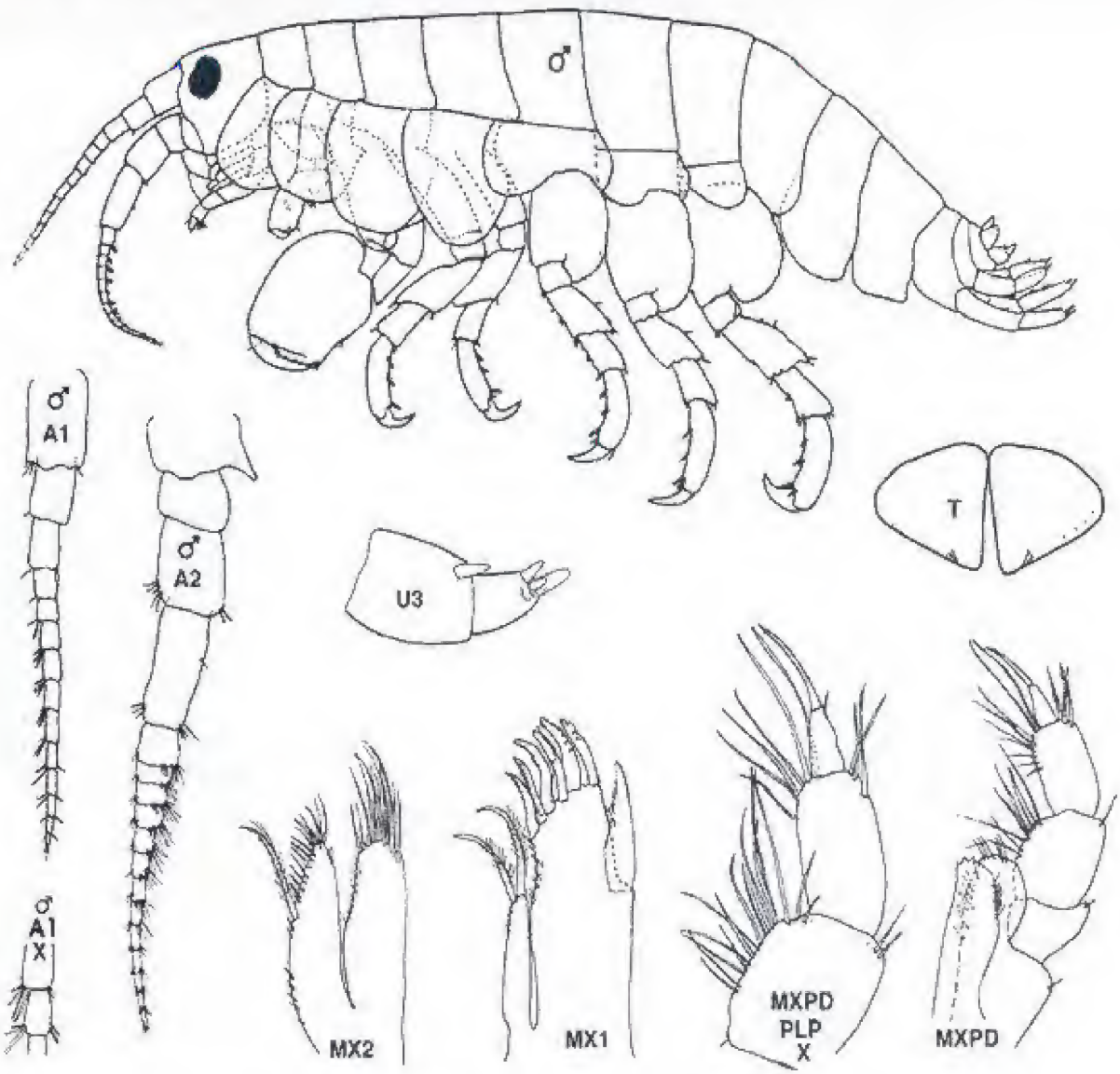

Fig. 1. *Hyale pontica* Rathke, 1937. Male (8.5mm); female ov (6.0mm). Bosphorus. (Telson of male specimen from Genova, after Krapp-Schickel, 1991).

Type locality: Krym (Crimea, Black Sea).

Material examined:
Cala Dragonara, NW Sardinia, stiff *Cystoseira* (brown alga), 0 m - ♀ (5.5 mm), 2 juv., MCSN slide 1901; Cala Dragonara, NWSardinia, 0 m. - ♂ (6 mm), MCSN slide 1902.
Bosphorus, Turkey - ♂ (8.5 mm) slide; ♀ ov. (6 mm) (alc).

Diagnosis: Male (9 mm). Eyes round, dark. Antenna 1, flagellum 10- 11-segmented, middle segments with aesthetascs in small clusters. Antenna 2, peduncular segment 5 > segment 4; flagellum 12-14-segmented, posteroproximally with clusters of short dense setae.

Mandibular left lacinia 5-dentate. Maxilla 1, strong ciliated setae on inner plate much surpassing end of outer plate. Maxilla 2, strong ciliated seta of inner plate surpassing inner end of inner plate. Maxilliped palp, dactyl with slender elongate unguis; propod and carpus subequal in length, width about 2:3; carpus on inner side with many long setae; merus short, as wide as carpus, but half as long; basis not much shorter than ischium.

Coxae 1-4, lower margin moderately crenulated ; Coxa 1 subrectangular, smooth behind. Coxae 2 & 3 with low but distinct posterior marginal cusps, lower margins gently convex. Coxa 4, hind margin excavated proximally, with median weak cusp . Coxa 5 moderately anterolobate. Coxa 6 weakly posterolobate.

Gnathopod 1, basis and ischium with very weak hydrodynamic lobes; carpus with small posterior lobe, not extending beyond merus, lower margin with ~4 comb setae; propod with strong mediofacial guiding

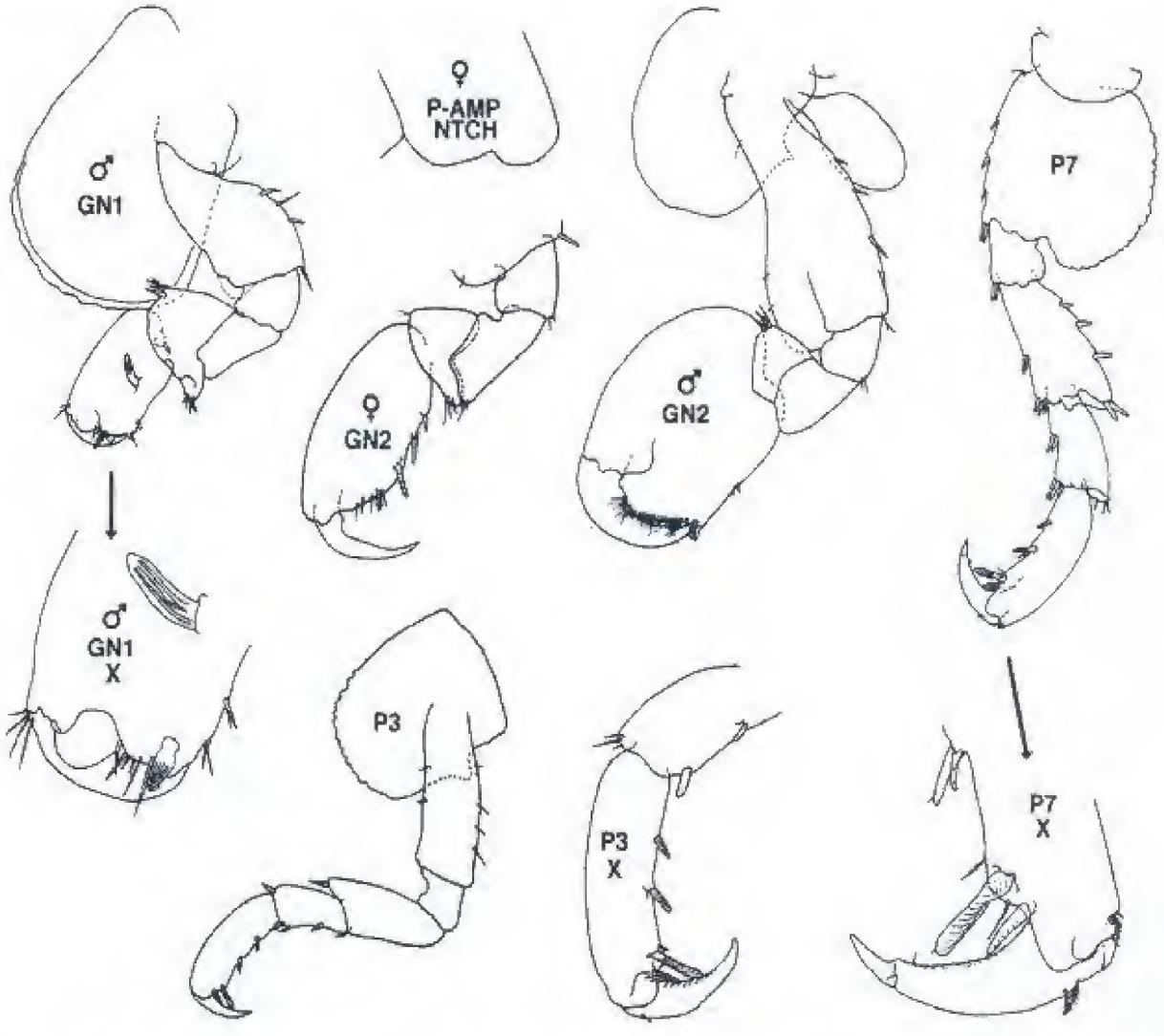

Fig. 2. *Hyale pontica* Rathke, 1937. Male (8,5 mm); female ov (6.0 mm). Bosphorus.

spine slanted slightly diagonally proximad, palmar locking spine stout, spade-shaped, slightly exceeded by tip of basally thickened dactyl. Gnathopod 2, hydrodynamic lobe very large and broadly rounded on basis, medium large on ischium; carpus short, lacking posterior lobe; propod subrectangular, slightly narrowing distally, hind margin with 1-2 short spines, palm convex, nearly transverse, lined with dense fine setae, and paired posterodistal short spines; dactyl stout, smooth, regular.

Peraeopods 3-4, segment 5 medium short; segment 6 with 2 proximally positioned posterior marginal spines and characteristic distal large cylindrical striated spine; dactyls stout, with minute inner marginal seta. Peraeopods 5-7 stout; basis widened, rounded, with clearly developed postero-distal lobe, hind margin with posterior notch and surge seta; segment 4 slightly widening distally; segment 5 not broader than long; segment 6 (propod), anterior (inner) margin with 2 proximal spines and distal stout striated clasping spine and supernumary shorter spine separated from it by a seta, with very short, distal "palm" set at 45° angle to axis of propod.

Epimeral plate 1 rounded behind; plates 2 and 3, posterodistal corner nearly right-angled. Uropod 1, peduncle slightly longer than rami, margins with 1-2 short robust spines. Uropod 2, rami short, subequal to peduncle, with 1-2 marginal spines. Uropod 3, peduncle with strong posterodistal spine; ramus ~2/3 length of peduncle, oblique apex with one strong robust spine, and two smaller ones.

Telson lobes broader than long, outer margin proximally with short setules and subapically with small spine.

Female ov (6 mm). Gnathpods 1 & 2 subsimilar, Gathopod 2 slightly the larger, with small hydrodynamic lobe on basis; propod subovate, palm oblique, posterodistal spines unequal, separated; hind margin

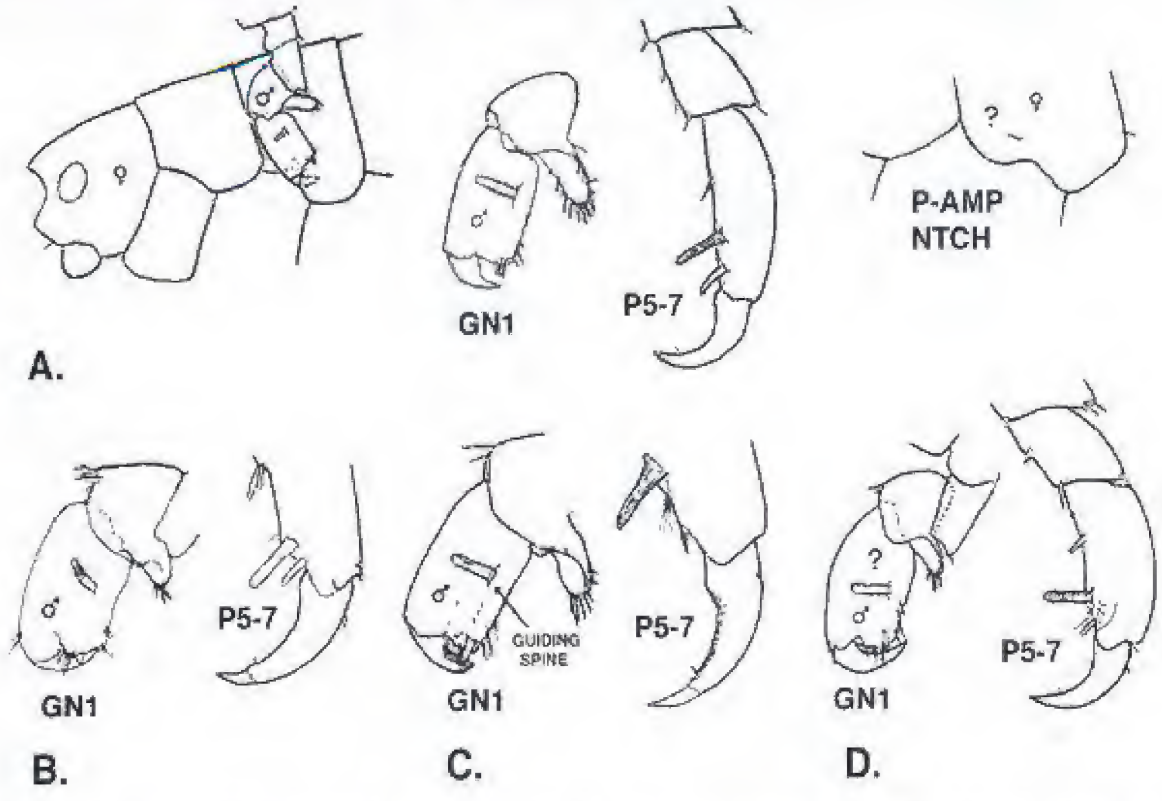

Fig. 3. Preamplexing mechanism in *Hyale* spp. A. *Hyale lubbockiana* Bate (female modified from G. O. Sars (1890); male gnathopod 1 in preamplexing position; B. *Hyale pontica* Rathke; C. *Hyale* sp. Bermuda; D. ***Hyale michelini*** n. sp (modified from Giovaninni 1965).

with 2 spines; dactyl slender, slightly overlapping palm. Brood plates broadly subovate, rounded apically. Preamplexing notch squared, with shallow posterodistal lobe and small locking slit near distal margin of anterior lobe into which fits the guiding spine of gnathopod 1 (♂).

Distributional Ecology: Exposed rocky coasts of the Mediterranean, Bosphorus, and Black Seas: among algae, littoral to infralittoral; not common. Not confirmed from the open Atlantic coast where it appears to be replaced by *H. lubbockiana*.

Remarks: *H. pontica* has not been found in the Northern Adriatic Sea, despite careful sampling by several authors. Some Mediterranean endemics apparently live exclusively in the Adriatic Sea, whereas other endemics live everywhere else but there.

Previous treatments of *H. pontica* require clarification. Thus, Krapp-Schickel (1993 p. 735, fig. 503) illustrates gnathopod 2 of an obviously penultimate ♂. The other gnathopod 2 (same specimen) showed a much more transverse palm, well defined by a short robust spine on the palmar corner. Gnathopod 1 (♂) bears a stout "guiding spine" on the medial surface of the propod (not figured).

Bulycheva (1957, pp. 90-92, fig. 30) illustrates a maxilliped apparently of quite different form. The difference may be attributable to the position of the maxilliped within the buccal mass. Thus, the terminal segments of the palp may be turned or twisted at a right angle to the vertical basal plates on the slide, and their size in the illustration would depend on the amount of pressure on the cover slip during preparation. On the other hand, Bulycheva's material (not examined in this study) may represent a different taxon. Her specimens apparently have less stout peraeopods, and the male gnathopod is of rather different form than material from the Mediterranean and Bosphorus regions.

Hyale lubbockiana (Bate)
(Figs. 3, 4, 5)

Galanthis lubbockiana Bate, 1856: 57 t. 17 f. 7;—Bate 1857:136;—Bate, 1862: 51, fig. VIII/3.
Nicea lubbockiana Bate & Westwood 1863: 47.
Hyale lubbockiana G.O. Sars 1890: 27, pl. 11, fig. 2;—Bousfield & Hendrycks 2002:100, figs. 46, 47.
Hyale pontica Lincoln 1979; 237, figs. 109e-j.

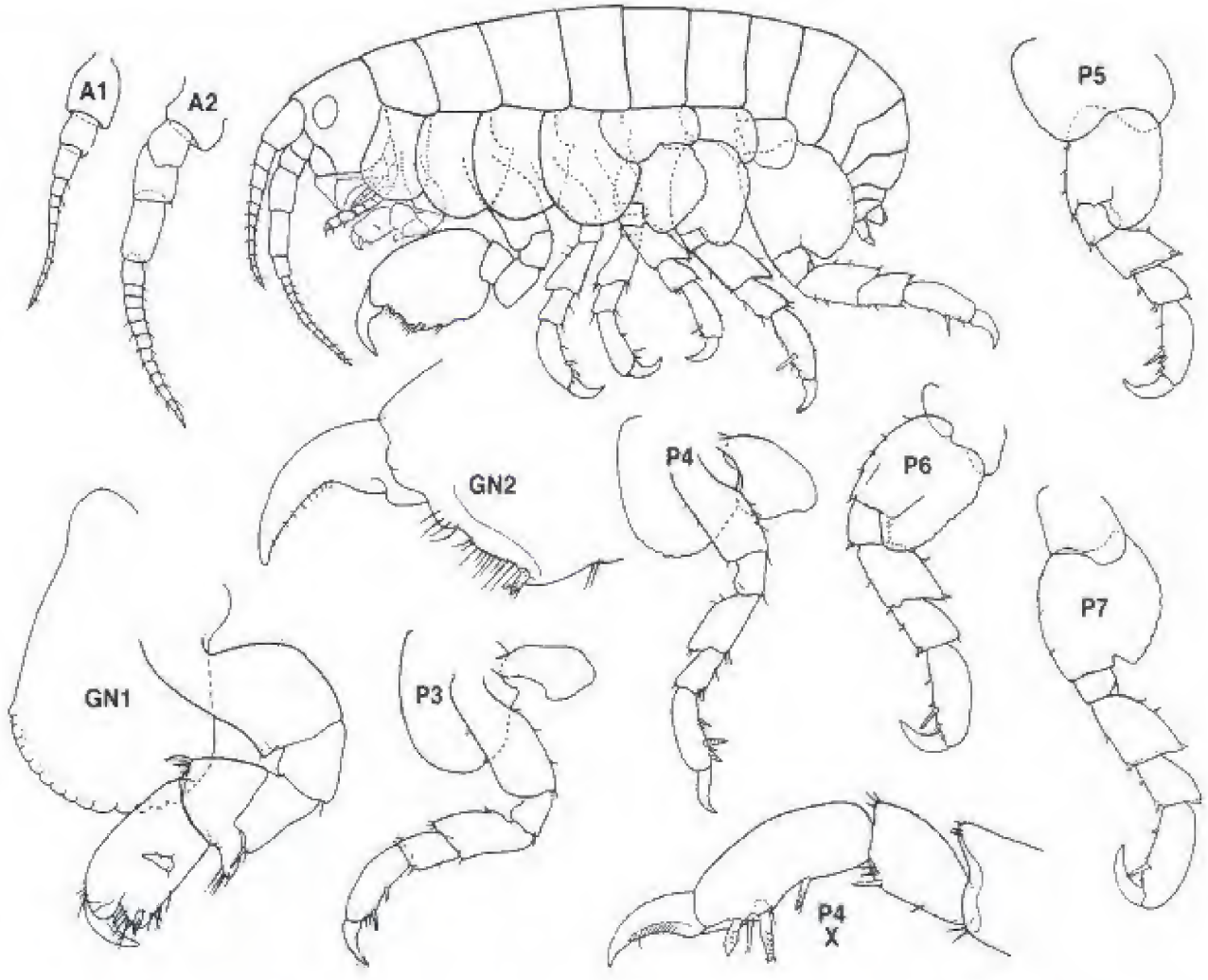

Fig. 4. *Hyale lubbockiana* Bate, 1856. Male (6.6 mm). Lofoten Ids., Norway.

Type locality: Falmouth, Cornwall, Great Britain.

Material examined:

Norway: Lofoten Islands, 0 m, W. Vader coll..- 2 ♂♂ (6.0 and 6.6mm), 2 ♀♀ ov (5.0 mm). Trømso Museum collns.

Great Britain: Port Erin, Isle of Man, in algae at LW, D.I. Williamson coll., March, 1955 - ♂ (7.5 mm); ♀ ov. (4.5 mm); CMN collections.

Diagnosis: Male (8 mm). Eyes round-ovate, pale-red. Antenna 1, flagellum 8-10 segmented. Antenna 2, flagellum 12-14 segmented, each with short single seta.

Mandibular left lacinia 5½-dentate. Maxilla 1, strong ciliated setae on inner plate short, not surpassing base of spine teeth of outer plate. Maxilla 2, inner marginal ciliated seta short, not reaching apex of plates. Maxilliped palp, unguis not attenutated, shorter than body of dactyl; propod and carpus relatively stout.

Coxa 1, lower margin strongly rounded and markedly crenulated. Coxae 2 & 3 with rounded hind marginal cusps. Coxa 4 posteroproximal margin with distinct median cusp.

Gnathopod 1, hydrodynamic lobe on basis and ischium very weak; carpal lobe relatively large, extending beyond merus, distally with ~6 comb setae; propod subrectangular, mediofacial guiding spine perpendicular or angled slightly distad. Gnathopod 2, hydrodynamic lobe of basis medium large, of ischium medium; propod deeply subovate, palm slightly oblique, with shallow rounded hinge tooth, beset with short setae, paired posterodistal spines short; propod hind margin distally with pair of fine setae; dactyl basally stout, hind margin lined with fine setules.

Peraeopods 3 & 4 prominent, regular; segment 5 short; segment 6 with one posterior marginal spine proximal to stout striated clasping spine that is separated from a short distal supernumerary spine by a single short seta; dactyl strong, moderately curved.

Peraeopods 5-7 strongly developed, hind margin of basis scalloped or crenulated, each with medium notch

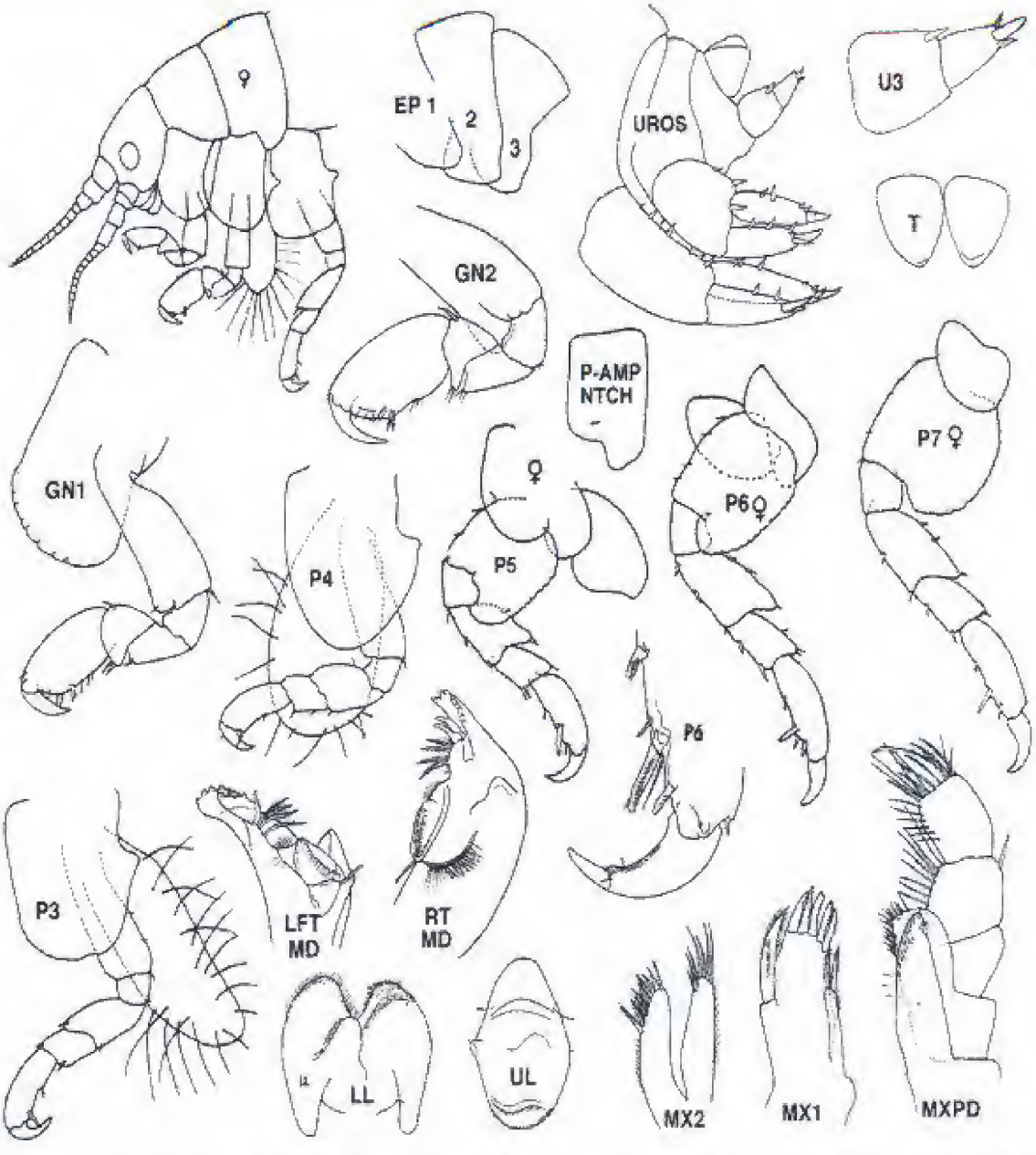

Fig. 5. *Hyale lubbockiana* Bate, 1856. Male (6.6 mm); female ov (6.0 mm). Lofoten Islands, Norway.

and surge seta; bases of peraeopods 5 & 6 with deep rounded posterodistal lobe; segment 6 with single proximal spine and distally with large striated clasping spine set at right angles to the axis of segment 6. Peraeopod 5, segment 5 short, wider than long.

Epimeral plate 1, posterior margin rounded; plates 2 and 3, hind corner slightly obtuse-angled. Uropod 1, peduncle deep, outer margin with several short spines; rami shorter than peduncle, with 2-3 short marginal spines and long and short apical spines. Uropod 2, peduncle short, deep; rami subequal to peduncle, each with 2 marginal spines and short and long apical spines. Uropod 3, peduncle with single stout posterodistal spine; ramus slightly shorter than peduncle, apex with one strong prominent spine and 2-3 shorter spines.

Telson lobes subtriangular, longer than wide, margins smooth, apex sharply rounded.

Female ov (6 mm): Gnathopods 1 & 2 subsimilar, 2 somewhat larger. Gnathopod 1, hydrodynamic lobe small on basis and ischium; carpus short, posterior lobe small; propod subovate, palm short; dactyl short, thick. Gnathopod 2, hydrodynamic lobe medium large on basis, lacking on ischium; carpal lobe small, narrow; propod, hind margin medially with 3-4 short setae. Brood plate (gnathopod 2) elongate, medium broad, apically rounded; marginal brood setae longer than half

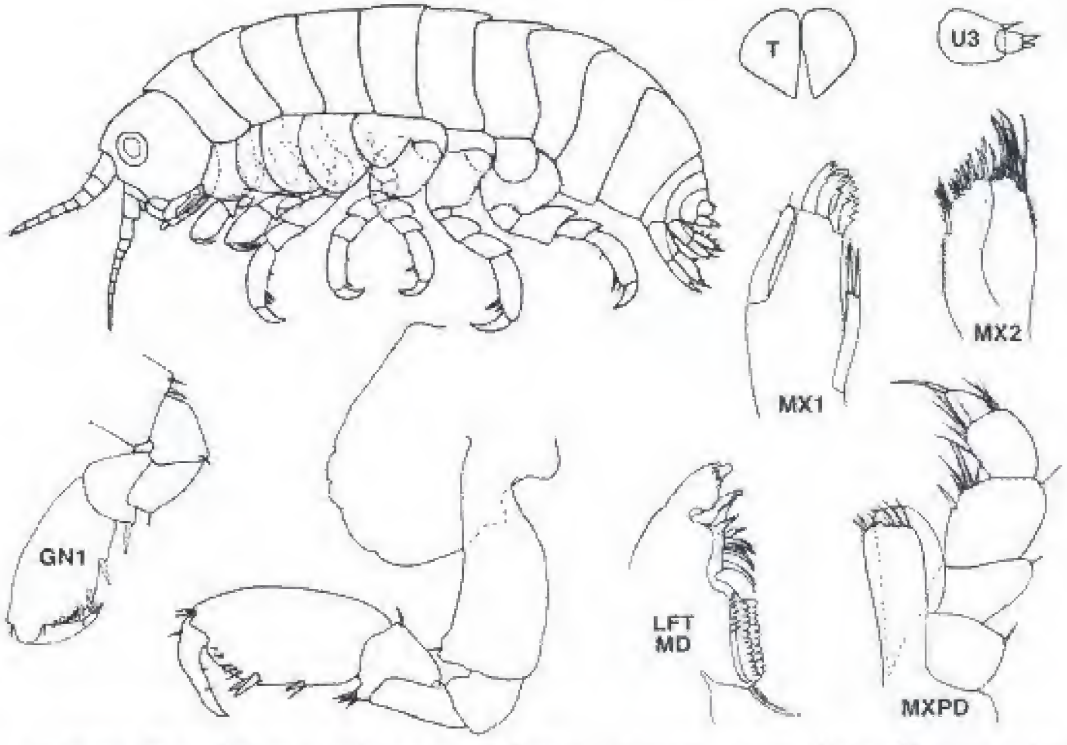

Fig. 6. ***Hyale michelini*** n. sp. Immature (3.5 mm). Capo Caccia, Sardinia (Mediterranean).

width of plate. Preamplexing notched squared; small locking slit on anterior lobe, above ventral margin. Colour: brownish-green (Lincoln, 1979 p. 236).

Distributional Ecology: Along exposed coasts of the temperate North Atlantic region, western France and the Irish Sea to northern Norway, amongst algae in rock pools in the lower half of the intertidal, from MSL to MLWS, to depth of about 50m (Lincoln, 1979; Vader:1971). All collections (*H. pontica* =H. *lubbockiana*) are from exposed rocky shores among intertidal algae, chiefly *Corallina officinalis* L.

Remarks: Bate & Westwood (1861, p. 48) described peculiar T-like marks on the integument. SEM pictures might clarify them but are not available. *H. lubbockiana* differs from *H. pontica* in its weakly setose antenna 2 (♂), normally unmodified condition of the dactyl of the maxilliped palp, and the vertical position of the large mediofacial spine of the propod of gnathopod 1 (♂). In addition, segment 5 of peraeopods 5-6 is short (width nearly equal to length), and the apical margins of the telson lobes are unarmed.

***Hyale michelini* n. sp.**
(Figs. 3, 6, 7)

?*Hyale pontica* Chevreux & Fage 1925: 283, fig. 294;—Giovannini 1965: 288-290, figs. 5-7.

Type locality: Capo Caccia, North Sardinia.

Material Examined:
Sardinia: Capo Caccia, 25 m, *Halimeda*, June 3, 1974 - immature (3 mm) **Holotype**; Capo Caccia, 0-1 m, interstitial and incrustation of *Balanus* - 2 imm (2.5-3mm) **Paratypes**; Capo Caccia, 15 m, *Posidonia*, June 3, 1974 - 3 imm (2.5-3 mm; Capo Ferrato, 10-22 m, among mixed algae, Schiecke coll., June 7, 1974 - 1 spec. (3 mm), MSNV collections.

Diagnosis: Male (5-6 mm)(after Giovannini, 1965). Eyes round, dark. Antenna 1, flagellum 9-10-segmented. Antenna 2, flagellum 13-14-segmented, segments each with single seta.

Mandible, left lacinia 5½-dentate; spine row with 3-4 blades. Maxilla 1, apical plumose setae of inner plate exceeding base of spines of outer plate; palp slightly exceeding base of spine-teeth of outer plate. Maxilliped palp, unguis slender, longer than body of dactyl.

Coxae 1-4 with rounded, crenulated lower margin. Coxa 1 subrectangular, smooth behind. Coxae 2 and 3, each with prominent posterior marginal cusp. Coxa 4 little deeper than 3, strongly rounded below, margin of posteroproximal excavation with weak median cusp. Coxa 5 markedly anterolobate. Coxae 6 & 7 posterolobate.

Gnathopod 1, basis and ischium with medium hydrodynamic lobe; carpal lobe small, with ~4 lower marginal setae; propod subovate, posterior margin with single median spine, mediofacial guiding spine un-

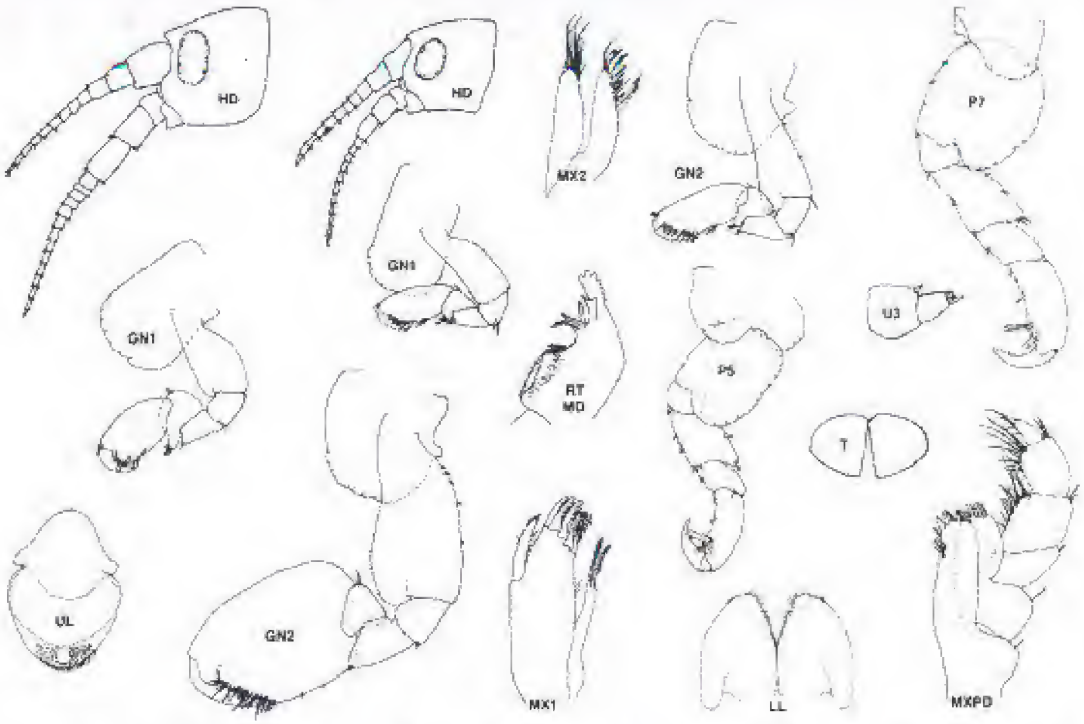

Fig. 7. ***Hyale michelini*** n. sp. Male (5-6 mm); female ov (4.5 mm) Among algae, LW. Marseilles, France. (modified from R. Giovannini 1965)

known; dactyl stout, tip slightly exceeding short, convex palm. Gnathopod 2, hydrodynamic lobe of basis medium strong, rounded, of ischium medium; carpus shorter than merus; propod deeply subrectangular, slightly narrowing distally, lower margin with 1-2 small spines, palm short, nearly vertical, lined with slender spines; dactyl regular.

Peraeopods 3-7 stout, heavy. Peraeopods 3 & 4, segment 6, posterior margin with single proximal spine and stout striated clasping spine separated from its distal shorter supernumerary spine by 1-2 short setae; dactyl stout medium strongly curved. Peraeopods 5-7, bases unevenly widened, hind margins scalloped, with notch and surf seta, posterodistal lobes broadly rounded; segment 5 of peraeopod 5 short, broader than long.

Epimeral plate 1, posterodistal corner rounded; plates 2 & 3, hind corners nearly right-angled. Uropod 1 peduncle short, with a few short outer marginal spines; rami subequal to peduncles, with 1-2 short marginal spines, and long and short apical spines. Uropod 2, peduncle stout; rami slightly shorter, each with 1-2 marginal spines and unequal apical spines. Uropod 3 small; peduncle with single posterodistal spine; ramus short, length about half peduncle, with 2 apical spines.

Telson lobes broadly triangular, apices nearly right-angled, margins smooth.

Female ov. (4-5mm). Gnathopod 1, basis and ischium each with weak hydrodynamic lobes; carpal lobe short; propod subovate, palm oblique, hind margin medially with setae cluster; dactyl slightly exceeding palm. Gnathopod 2, basis with medium large hydrodynamic lobe; carpal lobe short, narrow; propod somewhat narrowly subovate, palm oblique, hind margin with single median cluster of short setae; dactyl slightly exceeding palm. Brood plates and preamplexing notch not described.

Colour: green-yellow, eyes whitish-pink (Chevreux & Fage 1925).

Immature specimens (3.5 mm). Immature material collected off Capo Caccia, Sardina, by TK-S, is not referable to *Hyale pontica* from the Bosphorus region (Fig. 6). It differs in the less distal and more perpendicular position of the main clasping spine on segment 6 of peraeopods 3-7 and the less elongate dactyl and unguis of the maxilliped palp. These character states are more similar to mature specimens from this general region figured as "*Hyale pontica*" by Giovaninni (1965) (Fig. 7) and by Chevreux & Fage (1925) from Port Vendres on the Mediterranean coast.

In addition to regular allometric growth differences in numbers of antennal flagellar segments, fewer number of spines and setae on appendages, and undeveloped secondary sexual character states of the gnathopods and peraeon 2, the immature differs in the undeveloped or partially developed hydrodynamic lobes of the

and peraeon 2, the immature differs in the undeveloped or partially developed hydrodynamic lobes of the gnathopods, and unusually large apical spines of uropods 1 & 2.

Distributional Ecology: Western Mediterranean region; apparently living interstitially in coarse sand, from 0 to 25m depth.

Etymology: The authors are especially grateful to Aldo Michelini, for creative solutions to virtually every problem concerning transport, human connections, shrewdness, and for his always wide and open heart. We are pleased to name this species in his honour.

Remarks: Description of a new species based mainly on immature material at hand involves some taxonomic risk. Relatively small differences distinguish *Hyale pontica* and *H. lubbockiana*. We noted also that *bona fide* specimens of *H. pontica* co-occur at the same locality (Capo Caccia, Sardinia), but were collected in short, stiff brown algae of the surf zone, whereas the presently described material occurred mainly in the interstitium or on epiphytes and *Balanus* spp. to depths of 25m. Separate taxonomic status of *H. michelini* would seem justified.

Illustrations of "*Hyale pontica*" provided by Giovannini (1965) are very detailed. In all significant taxonomic respects they correspond to our material. The long and slender propods of gnathopods 1 and 2 of ovigerous females appear to be diagnostic character states of *Hyale michelini*.

Descriptions and drawings by Chevreux & Fage (1925) do not entirely fit any of our species, as there are several differences which might have been omitted or actually lacking (e.g., cusps on posterior margins of coxal plates, clasping spine on gnathopod 1 (♂), only one group of spines on peraeopods 3-7 (inner margin of segment 6) or simplification of shape of coxae 5 and 7. The shape of antenna 2 (♂) (groups of dense setae) or sharply angled propodal palm of peraeopod 7 would suggest *Hyale pontica* , but only one group of spines on the inner margin of the propod is figured. The shape of gnathopod 2 (♂) is similar to *H. lubbockiana* or *H. michelini*, and the body length applies to all of them.

Hyale sp.
(Figs. 3, 8)

Hyale sp. (MS name, CMN collections)
non: *Hyale pontica* Kunkel, 1910: 69, fig. 26.

Material Examined:
St. Georges, Bermuda, LW surf, A. W. Cameron coll., April, 1955: - male (7 mm) **Holotype** (slide mount); female ov (6 mm) **allotype** (slide mount); CMN collections.
Note - partial illustrations made in 1982; specimens and slide mounts not relocated.

Partial Diagnosis: Male (7. 0 mm). With the characteristics of the genus. Body smooth, not imbricated.

Maxilla 1, outer plate, apical armature encompasses an outer group of 6 stout distally pectinate spine teeth, and an inner group of three slender pectinate spines. Both the palp, and apical plumose setae exceed the base of the spine teeth of the outer plate.

Coxal plates 2 & 3 with posterior marginal cusp.

Gnathopod 1 (♂), carpus with large posterior lobe, exceeding merus, distal margin lined with 6-7 comb setae; propod evenly subrectangular, posterior margin with 2-3 distal clusters of short setae, mediofacial spine perpendicular or angled slightly distad, palm short, nearly straight, with stout posterodistal locking spine, slightly exceeded by tip of short stout dactyl.

Peraeopods with single stout grooved anterior marginal clasping (locking) spines, separated from distal supernumerary short spine by cluster of several short setae, palm scarcely distinguishable at steep angle to long axis of segment 6; dactyl gently curved.

Female: Undescribed. Gnathopods, brood plates and preamplexing notch characteristic of genus *Hyale*.

Distribution: Clinging to algae and other substrate in lotic waters of the surf zone, in the vicinity of St. Georges, Bermuda.

Remarks. On character states of gnathopod 1 and peraeopod segment 6, this species is clearly a member of the *pontica* group of hyalid amphipods. Full description and formal naming of the species awaits acquisition of additional material.

S. E. Johnson (1986) has synonymized Kunkel's material with *Parhyale hawaiensis* (Dana, 1853). Material of the latter species from beach drift at Hungry Bay, Bermuda, has been carefully figured by Stock (1987) and bears a remarkable similarity to "*Hyale pontica*" of Kunkel (loc. cit., fig. 26). Furthermore, photographs of Kunkel's figured male specimen and appendages , kindly provided by Dr. Eric Lazo-Wasem (YPM), leave little doubt that *Parhyale*, and not *Hyale*, is the genus in question.

In addition to *Parhyale hawaiensis*, widely distributed in tide pool drift debris (Johnson 1986; Stock 1987), and *Hyale* sp. from lotic water habitats at LW

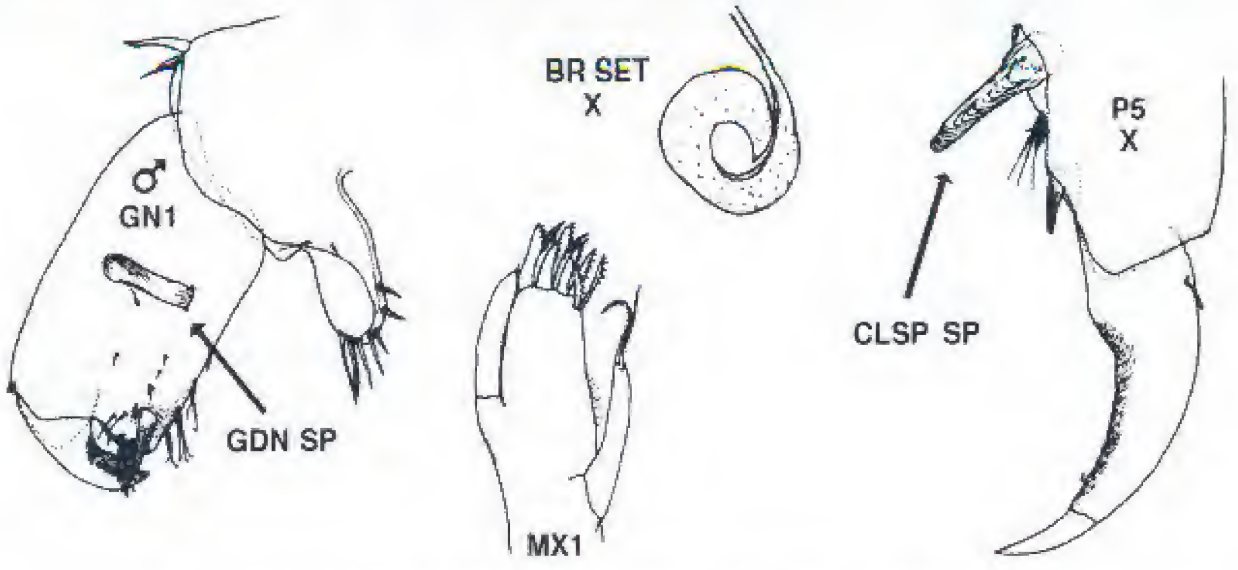

Fig. 8. *Hyale* sp. St. Georges, Bermuda, surf zone, LW.

level near St. George's, two additional hyalid species have been identified in CMN collections from Bermuda:

(1) A species of *Protohyale*, erroneously attributed to *Hyale pontica* by ELB, having stout distal peraeopodal clasping spines, elongate antenna 2, and uropod distolateral spine, occurs in LW pools at Outer Castle Island.

(2) A small saltating species of *Apohyle* occurs commonly in supralittoral tide pools at Devonshire Bay.

Discussion

Comparison of principal taxonomic character states within genus *Hyale* Rathke sens. str. (Table I) suggests that the four known species may be divided into two principal subgroups: (i) *pontica* subgoup, and (ii) *lubbockiana* subgroup.

The former consists of the single relatively advanced generic type species, *H. pontica*. The latter encompasses the three more primitive species, *H. michelini* n. sp., *H. lubbockiana*, and *Hyale* sp., of which *H. lubbockiana* entrains the greatest number of plesiomorphic character states.

As noted in the key and in Table I, *Hyale pontica* is especially distinctive in character states of gnathopod 1 (♂); distal position and oblique angle of clasping spine and angled "palmar" margin of peraeopods 3-7; and strongly setose flagellum of antenna 2 (♂). It shares relatively few character states with *H. lubbockiana* which, in view of previous confusion of the two species by several authors, is a somewhat surprising revelation of this study.

Bousfield & Hendrycks (2002, p. 124) have performed a semiphyletic cluster analysis of 11 of the 12 known genera within family Hyalidae. In balance of character states, the genus *Hyale* is relatively advanced but quite distinct from all other genera. It is perhaps least remote from the *Apohyale* complex, but is specialized for a life style in open lotic waters. Such features include the unique form of guiding and locking spines on the propod of gnathopod 1(♂), and corresponding preamplexing notch and locking slit of peraeon 2 (♀); well-developed hydrodynamic lobes of gnathopod 2; strong dactyls and strong clasping spines of peraeopods 3-7; and rounded form of epimeral plate 1.

The ancestry of genus *Hyale* remains moot. Although component species are "swimmers", the balance of character states suggests a relatively close relationship with genus *Apohyale*, especially with the subgroup of *A. prevosti (nilssoni)* in which hydrodynamic lobes of the gnathopods are strongly developed, and distal spines on the peduncle of uropod 1 are not strongly developed. On a somewhat broader phyletic basis, the form of the swimming species within Hyalidae, of which the life styles of genera *Hyale*, *Protohyale* and *Parallorchestes* are especially representative, reflects the basic hydrodynamic form of primitive "Natantia"(see also Bousfield and Hendrycks 2002).

On the other hand, the genus *Hyale* and especially species *pontica*, evinces similarities with the specialized hyalid subfamily Kuriinae. As noted in Bousfield & Hendrycks (2002, p. 119) character state similarities include subcarination and/or imbrication of body segments; crenulation of coxal and basal plate margins;

Table 1. Comparative Character States of *Hyale* species.

Character State	*H. pontica*	*H. lubbockiana*	*H. michelini*	*Hyale* sp. (Bermuda)
Length (♂, ♀)	6-9 mm	6-8 mm	4-6 mm	5-7 mm
A2 (♂), flag. setae	groups of many dense setae	few single setae	few single setae	few single setae
Mxpd palp, nail	> body of dactyl	< body of dactyl	>body of dactyl	?
Mx1, IP setae	surpassing OP spines	not surpassing OP spines	surpassing OP spines	surpassing OP spines
Mx2, IP seta	surpassing OP	not surpassing OP	not surpassing OP	?
Gn1 (♂), carpal lobe	small, few setae	large, 6+ setae	small 4 setae	large, 6+ setae
Gn1 propod (♂) mediofacial spine	slanted proximad	perpendicular	perpendicular ?	perpendicular
P3-7, palmar corner	~45°/vertical	15°/vertical	15°/vertical	15° /vertical
P3-7, inner marginal spines	2 groups proximal to clasping spine	1 group proximal to clasping spine	1 group proximal to clasping spine	1 group proximal to clasping spine
P5-7, dactyl curvature	weak	strong	weak	
U3 ratio: length peduncle:ramus	3:2	3:2	2:1	?
Distribution	Black Sea, Central Mediterranean	N. E. Atlantic	W. Mediterranean	Bermuda

presence of posterior marginal cusps on coxae 2 & 3 only, and specialized form of the maxilliped palp. *Hyale pontica* also overlaps geographically with *Micropythia* and abuts the more southerly range of *Kuria longimanus*.

The four known species of genus *Hyale* exhibit a relatively restricted geographical distribution. Species are confined to high salinity outer coast lotic water swash zones of temperate and subtropical NE Atlantic and Mediterranean regions. However, these habitats are relatively poorly collected and studied. Further records might be anticipated from open ocean coasts of Spain, Portugal, and island archipelagos off the coast of North Africa, including the Canaries and the Azores.

Myers' (1991) analysis of family groups within corophioidean and melitoidean amphipods of the Hawaiian Archipelago underscores the need to consider phyletic age of a taxonomic group as a factor in developing hypothetical dispersal patterns and biogeographic faunal relationships. Character state analysis suggests that within family Hyalidae, members of genus *Hyale* are a relative recently evolved group of species. Their present confinement within the eastern North Atlantic and Mediterranean regions seemingly conforms with a relatively recent geotectonic origin of those basins during Cretaceous times (Howarth 1981).

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